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Developmental Differences Among Five Lodgepole Pine Provenances Planted on a Subalpine Site in Montana

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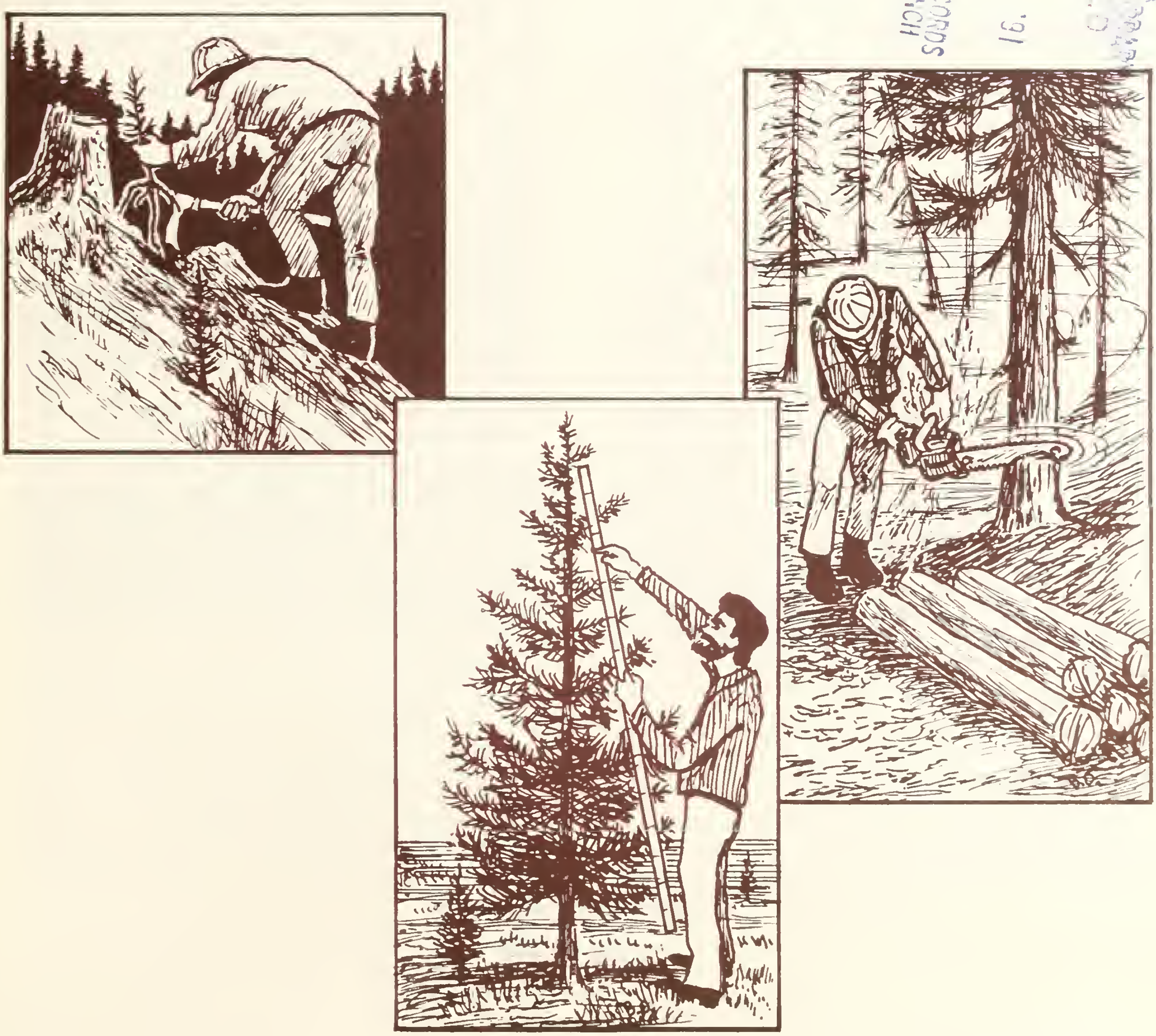

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RESEARCH SUMMARY

Developmental differences of progeny from lodgepole pine seed from British Columbia, Washington, Idaho, Utah, and a local population, were observed after 12 years in a provenance study conducted on a high-elevation site in southwestern Montana.

The short-term purpose of this study is to determine how these widely separated provenances of lodgepole pine differ in early expression of tree development and in variation of form among and between families. The long-range goal is to ascertain whether yield of lodgepole pine can be improved in this high-elevation Montana habitat by planting trees from distant populations that are cold acclimated but might differ in adaptation to length of growing season.

Seedlings from six to 10 families from each provenance were grown in the nursery to provide 3-0 stock for planting at the study site in the Gallatin National Forest in Montana. The study site is located at 6,600 ft (2,200 m) elevation, has a frost-free season of about 50 days, and receives about 30 inches (76 cm) of annual precipitation. From four to 10 offspring of each family were planted in consecutive planting spots in randomly allocated row plots. Distance between rows and trees within a row was 10 ft (approximately 3 m).

Mortality was recorded and total heights and lengths of terminal leaders of trees were measured in 1976, 1978, 1979, 1982, and 1987. Crown width was measured in 1982 and 1987. Diameter at breast height and heights to the lowest live limb, base of the balanced crown, and to the widest part of the crown were measured in 1987.

Survival was analyzed with chi-square procedures, and provenance differences in various growth characteristics were determined by analyses of covariance, using either initial height of seedlings at time of planting or the previous year's total height as covariates, where appropriate. Least-square means procedures were used to adjust for unequal numbers of families within provenances and seedlings within families. Probabilities of difference in least square means were used to determine statistical differences among the provenances in their various growth expressions and to compare provenances for relative degrees of among- and within-family variation.

Survival differences among the provenances after 12 years were found to be statistically nonsignificant at the 0.05 level, suggesting that any provenance differences in development of surviving trees that might occur would be likely to be influenced by other genetically controlled traits than by cold intolerance alone. After 12 years, trees of the Idaho provenance have become as large, or larger, than all other provenances in height, diameter, and crown width—and show the greatest degree of crown recession. The British Columbia and Washington provenances followed in magnitude of these developmental characteristics, but differences with the Idaho provenance were not statistically significant, except for the lower crown widths of the Washington provenance. The local Montana provenance was generally intermediate in all characteristics except crown recession, in which it had the least. The Utah provenance showed the least development in height, diameter, and crown widths, but had consistently the highest levels of within-family variation for all growth expressions measured. Patterns of among-family variation among the provenances differed from growth expression to growth expression, but overall the Washington population exhibited the most variation among families, and Montana the least.

The performance data and relative indicators of genetic variability developed in this study should be useful in selecting genotypes for improved yield performance in this and similar habitats. After 12 years of comparison, the Idaho provenance tested here appears to offer the greatest potential for timber management, but genotypes of other provenances might be selected to emphasize other traits, such as slower crown recession for retaining hiding and thermal cover longer in stands—an important consideration in wildlife management.

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INTRODUCTION

Harvesting of lodgepole pine (*Pinus contorta* var. *latifolia*) is usually done by clearcutting and the harvested area is usually regenerated naturally from the local seed source. However, natural regeneration sometimes fails when site scarification is inadequate or when logging and silvicultural activities are not coordinated with the level of cone serotiny in the stand. In these cases, the site is usually planted using seedlings from a nearby seed source. Recent studies suggest, however, that improved growth and yield is possible from alternative seed sources, judiciously chosen.

Perry and Lotan (1978), in a greenhouse experiment, found that seedlings from Washington, Idaho, and British Columbia seed were taller and heavier than those from high-elevation seed from Montana and Utah, although differences in response to day-length and temperature were not significant. Illingworth (1975) found that early height growth and frost resistance differed among 144 lodgepole pine provenances planted at coastal and inland locations in British Columbia, and suggested that distant populations might be grown successfully in continental climes if sufficiently adapted to cold. Subsequent studies have clearly shown that adaptation in lodgepole pine is closely related to environmental variables (Critchfield 1980; Rehfeldt 1987; Rehfeldt and Wykoff 1981). Rehfeldt and Wykoff (1981) found that genetic differences in height growth, among 30 lodgepole pine populations from widely different elevations of Idaho and Montana, were expressed through adaptation of shoot elongation to the length of the growing season, rather than to the noticeably different temperatures alone. Correspondence of variation in shoot elongation with variation in freezing tolerance was interpreted as evidence that height growth of lodgepole pine populations is coordinated with cold acclimation through adaptation to the length of the growing season. More recently, Rehfeldt (1983, 1986, 1987) in a series of seedling studies has described the adaptation potential of Rocky Mountain lodgepole pine populations for cold hardiness, growth potential, and insect and disease resistance, and developed guidelines for determining seed transfer limits.

On the basis of the availability of wind-pollinate seedlings from the same parent trees used in Perry's greenhouse experiments, I decided in 1975 to evaluate long-term field performance of those geographically distinct populations when planted in a cold, high-elevation Montana environment representing a large area of the *Abies lasiocarpa* climax series where lodgepole pine is a dominant forest cover type. Early survival and growth differences among the five provenances were reported through the seventh growing season (Cole and McCaughey 1984). This paper reports sapling-stage development through 12 growing seasons and how different growth expressions vary among and within provenances and families.

STUDY DESCRIPTION

Study Site

The study site is located near Rat Lake—Squaw Creek drainage, Gallatin National Forest, Montana—in a clearcut area harvested in 1970. Lodgepole pine was the major species in the harvested stand, with a small proportion of Engelmann spruce (*Picea engelmannii* Parry) distributed throughout the area. Site index (base 100) for lodgepole pine is between 60 and 70 ft (18 and 21 m) and elevation is about 6,600 ft (2,000 m) above sea level. The ecological habitat type (Pfister and others 1977) is *Abies lasiocarpa/Linnea borealis*. Prominent understory species at the time of harvest were *Linnea borealis, Vaccinium caespitosum*, and *Calamagrostis canadensis*.

The soil in the study area is developed to 18+ inches (46+ cm) and is classified as a silt loam of the Cryochrepts-Cryoboralfs-Lithic Cryoborolls group of the Inceptisol-Alfisol association (USDA Soil Conservation Service 1978). The study area lies across a gentle draw midway on a gentle north-facing slope. The site is quite moist into July of most years. No weather data are available for the specific site, but annual precipitation is judged to be a few inches greater than the 30 inch (76 cm) average recorded at the Squaw Creek Ranger Station, located about 4 mi (6.4 km) down the drainage at about 1,200 ft (365 m) lower elevation. The average length of the freeze-free season is about 50 days (Caprio 1965).

Seedling Origin, Propagation, Planting

Seed was collected from 10 parent trees in each of five widely separated stands in Utah, Montana, Idaho, Washington, and British Columbia. Locations, latitudes, elevations, habitat types, and site indexes of the stands are shown in table 1. Stands were selected from similar ecological habitat types (Daubenmire and Daubenmire 1968) to represent, as much as possible, reasonably similar growing opportunities for lodgepole pine. In this regard, the effects of shorter and cooler growing seasons at the higher elevation Montana and Utah sites were assumed to be somewhat offset by greater growing season precipitation than commonly occurs at the Idaho, Washington, and British Columbia sites (Perry and Lotan 1978).

Seedlings were grown at the Lucky Peak Nursery near Boise, Idaho, and planted as 3-0 stock on the study site in the spring of 1975. Seedlings were lifted from the nursery before spring growth began in 1975, bundled by parent tree identity, and placed in cold storage until the study site was accessible.

On June 9-10, 1975, 284 seedlings, representing from four to 10 offspring of each mother tree, were planted in 13 rows of a 0.75-acre (0.3-ha) plot. Rows were spaced 10 ft (~3 m) apart and trees were spaced 10 ft (~3 m) apart in the rows. Planting spots were grouped by parent tree—that is, all seedlings from a given parent were planted in a row plot (consecutive planting spots in a row)—but the row-location of parent-groups was randomized. The planting could have been randomized to the individual-tree level, but this would have required unacceptable handling and delay in separating and randomizing the seedlings to that level—risking study confounding from planting effects. Therefore, seedlings were randomized only to the parent-group (family) level, planted, and identified by tagged stakes showing the provenance, parent tree, and individual tree numbers of each seedling.

Measurements and Analysis

Mortality was recorded, and total heights and terminal leader lengths were measured in centimeters—in 1976, 1978, 1979, 1982, and 1987. Codes were used to identify healthy versus unhealthy trees and those with damaged versus undamaged leaders. Crown width was added to the measurements in 1982 and 1987; and diameter at breast height and heights to the lowest live limb, base of the crown, and to the widest part of the crown, were measured in 1987.

Data were analyzed with the chi-square test for differences in survival and frequency of damaged or unhealthy trees, and by analysis of covariance for differences in growth between the provenances.

Although differences in the frequency of unhealthy and damaged trees among the provenances were highly insignificant, according to the chi-square test, only healthy, undamaged trees were included in the growth analyses.

The initial height of seedlings at the time of planting was used to adjust the provenance means of the various growth expressions. A covariance model of the form $Y = b_0 + b_1$ Provenance + b_2 Initial Height was used to evaluate the influence of provenances on growth. The covariate, Initial Height, was found to be independent of provenances for all growth expressions; therefore, interaction effects between provenances and initial heights was not involved in the analysis. Another coveriance model of the form $Y = b_0 + b_1$ Parent + b_2 Initial Height was used to evaluate the significance of variation in the various growth expressions due to parents (families) within provenances.

Although the overall F test for provenance means in the analysis of covariance was not particularly significant for some growth expressions in 1987, pairwise comparisons can be made to test partial null hypotheses in which some means are equal but others differ (SAS Institute 1985).

Table 1—Location and site characteristics of stands providing seed for provenance study

Stand	Location	Elevation		Habitat type	Site index (Alexander 1966)
		Ft	*m*		
Washington	Sherman Pass, Colville N.F., lat. 48°36' N.	5,250	(1,600)	*Abies lasiocarpa -Pachistima myrsinites* (Daubenmire and Daubenmire 1968)	90
Montana	Butte Meadows, Gallatin N.F., lat. 45°26' N.	7,220	(2,200)	*Abies lasiocarpa -Galium triflorum* (Pfister and others 1977)	80
Utah	Gilbert Creek, Wasatch N.F., lat. 40°54' N.	8,200-9,150	(2,500-2,790)	*Abies lasiocarpa/Berberis repens* and *Abies lasiocarpa/Vaccinium scoparium* (Pfister 1972)	45
Idaho	Little Slate Cr. Nez Perce N.F., lat. 45°40' N.	5,100	(1,550)	*Abies grandis -Xerophyllum tenax* (Steele and others 1981)	90
British Columbia	Caribou Land District, lat. 53°25' N.	2,300	(700)	Unknown, but probably *Abies lasiocarpa/ Clintonia uniflora* (Daubenmire and Daubenmire 1968)	100

Accordingly, the least squares means (LSMEANS) method, with the probability of difference (PDIFF) option, of the General Linear Models (GLM) procedure of the SAS statistical program (SAS Institute 1985) was used to evaluate variation in the various growth expressions, among and within families and provenances. The SAS procedures provide methodologies for dealing with the unbalanced design of this study that were not before available and furnish a common basis for evaluating changes in the development of provenances between 1982 and 1987. Some of the 1982 measurements that were reported earlier (Cole and McCaughey 1984) were also reanalyzed with the SAS statistical program; however, interpretations were not changed by the reanalysis.

To evaluate among-family variation in tree development, I used p-values from the SAS General Linear Models PDIFF option described above and determined the proportion of possible family differences for each growth expression and provenance that had a 10 percent or less probability of occurring by chance. These proportions provided a relative means to compare provenances for extent of among-family variation in the various growth expressions measured.

Within-family variation was assessed by computing coefficients of variation for growth expression standard deviations (Steel and Torrie 1960) and comparing their relative magnitudes among provenances.

RESULTS AND DISCUSSION

Variation Among Provenances

Perry (1974) in his greenhouse study of the same wind-pollinated families tested in this provenance study found that British Columbia seedlings were consistently taller, Idaho and Washington were intermediate, and Utah and Montana formed a lower group—except under the two shortest day lengths where Utah and Montana trees were taller. With respect to growing period, there were significant differences among the provenances in reaction to day length, but not temperature. The significance of the day length-provenance interaction, however, was due primarily to the British Columbia seedlings, which when removed from the analysis resulted in a nonsignificant effect of day length on the other provenances. In the following sections, differences in survival, condition, and development of the provenances 12 years after planting, are discussed.

SURVIVAL AND TREE CONDITION

Mortality continues, but to a lesser degree and with less difference between provenances than observed earlier (table 2). A chi-square test of survival among the provenances through 1987 indicates that survival differences of the magnitude of table 2 would occur by chance about 70 percent of the time; therefore, survival among provenances after 12 years is not considered to be statistically significant. Similarly, a chi-square test of numbers of damaged and healthy trees in each provenance in 1987 indicated that such provenance differences would occur by chance about 87 percent of the time. Therefore, it appears that mortality to date has occurred randomly throughout the study area and has not been due to any particular factor. The varied mortality history of the study to date suggests that developmental differences between the provenances might also be significantly influenced by other traits in addition to cold acclimation.

Table 2—Number of trees planted and percentage of trees surviving in 1976, 1982, and 1987 by provenance

Provenance	No. trees planted 1975	Percent surviving 1976	1982	1987
Utah	63	90	83	81
Montana	51	90	88	82
Washington	46	87	78	76
Idaho	43	77	74	72
British Columbia	81	88	84	81
Total and percentage means	284	86	81	79

TREE DEVELOPMENT

Means of tree development measures for each provenance and year of measurement are summarized in table 3. Results of covariance analyses for evaluating provenance differences in early development are discussed immediately below, while evaluations of the relative variation among and within families and provenances, are discussed further along.

Height Growth—Total tree height increased markedly from 1982 to 1987 in all provenances (table 3); however, the significance of the overall F test for provenance differences in adjusted sapling heights declined appreciably (p values for the F test were 0.01 and 0.29, respectively). Nonetheless, pairwise comparisons of adjusted provenance means were made to determine if any provenances differed ($p < 0.10$) in heights in 1987. Least-squares means of heights in 1987 (H87) were estimated to account for unequal numbers of trees among the provenances, and used to test specific provenance differences in total height in 1987. In these comparisons, Idaho trees were significantly taller than Utah trees in 1987 ($p = 0.03$). No other differences were practically significant (p values > 0.20).

The greatest absolute height growth was previously in British Columbia trees; however, their annual percentage rate of height growth since 1982 has fallen behind all other provenances, and the Idaho trees are now virtually equal in total height with the British Columbia trees (table 3). In addition, although Idaho trees are still significantly taller than Utah trees, the height growth rate of Utah trees in the last 5 years has been greater (table 3). These results suggest that the patterns of height growth rates and attained heights among the provenances might be considerably different in the future.

Crown Width—Absolute crown widths were greatest in Idaho and British Columbia trees (table 3); but since crown width is strongly correlated with tree height, 1987 crown widths (CW87) were covariance adjusted for

Table 3—Periodic annual height growth percent, and means of: total heights, terminal leader lengths, heights to lowest limb, heights to crown base, crown widths, and diameters at breast height (d.b.h.)—by provenance and year of measurement

Provenance	Year	Height growth	Total height	Terminal leader length	Height, lowest limb	Height, crown base	Crown width	D.b.h.
		Percent	- - - - - - - - - -	- - - - - -	- - - - - - *Centimeters*	- - - - - -	- - - - - -	- - - - - -
Utah	1975	—	13.5	—	—	—	—	—
	1976	40.0	18.9	5.4	—	—	—	—
	1978	41.3	34.5	10.9	—	—	—	—
	1979	30.7	45.1	12.1	—	—	—	—
	1982	31.3	87.5	19.2	—	—	46.1	—
	1987	31.6	225.9	39.8	23.7	34.0	97.1	3.1
Montana	1975	—	13.0	—	—	—	—	—
	1976	43.8	18.7	5.7	—	—	—	—
	1978	48.4	36.8	11.0	—	—	—	—
	1979	31.5	48.4	12.9	—	—	—	—
	1982	46.9	93.8	21.5	—	—	53.3	—
	1987	32.4	245.6	38.8	20.7	32.3	105.5	3.6
Washington	1975	—	16.1	—	—	—	—	—
	1976	42.9	23.0	6.9	—	—	—	—
	1978	44.8	43.6	13.4	—	—	—	—
	1979	29.8	56.6	13.8	—	—	—	—
	1982	29.3	110.8	20.8	—	—	53.6	—
	1987	28.0	268.1	47.1	26.4	38.8	104.0	3.7
Idaho	1975	—	14.8	—	—	—	—	—
	1976	43.9	21.3	6.5	—	—	—	—
	1978	52.6	43.7	15.5	—	—	—	—
	1979	37.8	60.2	15.9	—	—	—	—
	1982	32.3	119.2	24.4	—	—	62.2	—
	1987	25.7	277.1	45.2	27.8	42.4	124.1	4.0
British Columbia	1975	—	19.4	—	—	—	—	—
	1976	40.2	27.2	7.8	—	—	—	—
	1978	52.5	56.0	17.6	—	—	—	—
	1979	29.5	72.5	18.3	—	—	—	—
	1982	28.0	133.4	24.4	—	—	69.7	—
	1987	21.6	277.5	42.4	23.2	37.4	121.5	3.8

current height (H87) to make provenance comparisons. The F test indicated highly significant differences in 1987 crown widths among the provenances, when adjusted to a common height in 1987 ($p = 0.0002$). According to pairwise comparisons of least-squares means, Idaho and British Columbia crown widths in 1987 were significantly greater for a given height than those of Montana, Utah, and Washington; while Montana was significantly greater than Washington (p values < 0.07—p values of all other comparisons > 0.22). This pattern of differences is appreciably different than in 1982, when crown widths for a given height were significantly greater for Montana and British Columbia trees than those of Utah (p values < 0.05).

Crown Recession—Heights to the lowest live limb (HLL87) and the base of the balanced live crown (HBC87) were measured in 1987 as indicators of crown recession and found to vary appreciably among provenances. The Montana population had the least recession in both lowest live limb and base of the balanced crown, British Columbia and Utah were intermediate, while the Idaho and Washington populations had the most (table 3). After covariance adjustment for initial height of seedlings when planted, variation due to provenances was found to be highly significant for both variables ($p = 0.01$ and 0.001, respectively), according to the F statistic. Pairwise comparisons of least-squares means indicate that differences between Montana versus Idaho and Washington trees were statistically very significant (p values ≤ 0.01). Several other provenance comparisons showed statistically significant, though lesser, differences.

Like Montana, Utah and British Columbia trees had markedly lower live limbs than Idaho trees ($p = 0.05$ and 0.02, respectively), but the only other difference in height of lowest live limb to approach those levels of significance was that between British Columbia and Washington trees ($p = 0.10$).

In heights of balanced live crowns (HBC87), the Montana population also showed significantly less recession than British Columbia ($p = 0.07$), as well as Idaho and Washington (as mentioned above). The Utah population also showed significantly less crown recession than Idaho and Washington trees (p values < 0.08), but were not greatly different than British Columbia trees in this regard ($p = 0.34$). The British Columbia trees were intermediate, in crown recession—and, although significantly greater than Montana trees, were significantly less ($p = 0.01$) than those of Idaho.

These provenance differences suggest that early crown recession is under genetic influence. Further evidence is provided in the discussion of tree development variation within provenances presented below.

Stem Diameter—Breast height (4.5 ft [1.37 m]) diameter (D87) of saplings was measured for the first time in 1987, when all but two surviving trees in the study had attained that height. Idaho saplings were the largest in absolute diameter in 1987, while Utah saplings were the smallest (table 3). British Columbia, Washington, and Montana saplings ranked behind Idaho in that order; however, when adjusted for initial seedling heights, stem diameters in 1987 showed a somewhat different pattern of differences in least-squares means than seen in table 3 for unadjusted means. Specifically, British Columbia and Montana switched places from the order shown in table 3. Statistically, comparisons of least-squares means showed that adjusted Idaho diameters were significantly larger than those of British Columbia and Utah, while Montana diameters were significantly larger than those of Utah saplings (p values < 0.10).

Variation Within Provenances

Perry (1974) found that wind-pollinated siblings of the families tested in this provenance study had a mixed pattern of variation among and within families, in response to day length. British Columbia seedlings had more variation within families than among them, while the opposite was true for Utah seedlings. Washington and Idaho seedlings had considerable variation both within and among families, while those from Montana seemed to have the least of both types of variation.

In this study, among-family differences in sapling development were evaluated by comparing, for various growth expressions, the proportions of possible family differences within-provenance that had p values ≤ 0.10 (table 4). Considering all growth expressions together (see last column, table 4), Montana saplings had much less variation among families, while Washington and Utah had the most. Because Utah seed was collected over a 850-ft (290-m) elevational range (table 1), variation among families would be expected to be greater than within families, as the likelihood of different ecotypes among the parent trees increased. But Washington seed was collected within a 10- to 25-acre (5- to 10-ha) area at the same elevation, so its among-family variation appears to be more a result of genetic variation. British Columbia saplings showed moderately low variation among families for all growth expressions. Idaho was generally intermediate among the provenances, except it showed relatively high among-family variation for height growth measures while showing the least in the crown recession variables HBC87 and HLL87. In contrast, the Utah saplings showed more variation among families in these two crown recession indicators than the other provenances combined—again, probably due to the wide elevational spread among the parent trees.

Table 4—Percentages of family differences, in least-squares means, having less than a 10 percent probability of occurring by chance

Provenance	Characteristic[1]							Average percent of family difference
	H87	L87	PHG	HLL	HBC	CW87	D87	
	Percent							
Washington	57	48	57	14	0	52	33	37.3
Montana	5	0	0	10	0	0	10	3.6
Utah	47	31	53	47	44	42	33	42.4
Idaho	47	47	27	0	0	20	7	21.1
British Columbia	13	18	16	4	18	20	11	14.3

[1]H87 = total height in 1987
L87 = leader length in 1987
PHG = periodic height growth in 1982-87
HLL = height to lowest live limb
HBC = height to base of balanced crown
CW87 = crown width in 1987
D87 = diameter at breast height in 1987.

Table 5—Coefficients of variation (CV) for within-family standard deviations of characteristics, by provenance

Provenance	Characteristic[1] H87	L87	PHG	HLL	HBC	CW87	D87	Average CV
Washington	50	49	43	28	39	26	81	45
Montana	32	41	34	29	40	30	20	32
Utah	47	48	44	51	43	70	50	50
Idaho	23	40	38	18	26	32	24	29
British Columbia	47	29	42	36	36	26	36	36

[1]H87 = total height in 1987
L87 = leader length in 1987
PHG = periodic height growth in 1982-87
HLL = height to lowest live limb in 1987
HBC = height to base of balanced crown in 1987
CW87 = crown width in 1987
D87 = diameter at breast height in 1987.

Within-family variation was evaluated for each provenance and growth expression by determining the coefficients of variation for standard deviations of families (table 5). No particular pattern of relative within-family variation among the provenances in individual growth expressions is evident in table 5, except for Utah, which had consistently high levels of within-family variation for all growth expressions. Unlike among-family variation, within-family variation of the Utah provenance would not be so likely to be affected by elevational differences among the parent trees. To assess relative degrees of within-family variation among provenances, all growth expressions were combined (see last column, table 5). On this basis, Utah saplings had distinctly greater variation within families than the other provenances, while Idaho and Montana had the least.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

After 12 years, earlier differences in survival and tree condition among the provenances have become statistically insignificant. Significant differences between provenances were found; however, for several developmental traits, as well as indications of differences between the provenances in among- and within-family variation.

Height growth differences among the provenances are declining, largely due to the slowest growing provenances beginning to catch up with the taller provenances. Only the tallest (Idaho) and the shortest (Utah) provenances were significantly different at year 12.

The pattern of height-adjusted crown width among provenances has changed considerably from year 7 to 12, with the previously widest Montana population dropping to intermediate position. Genetic differences in the crown width trait among lodgepole pine populations are highly correlated with those of tree height (Rehfeldt 1985); therefore, provenance means for crown width were evaluated with height held constant. The tallest provenances (Idaho and British Columbia) still had significantly greater crown widths for a given height than the Montana, Utah, and Washington provenances (p values < 0.07).

Crown recession differences among provenances were assessed for the first time at year 12, using measurements to the lowest live limb and to the base of the balanced live crown. Differences in provenance means were adjusted for seedling height when planted and found to be highly significant ($p < 0.01$) for both indicators of crown recession. The Montana provenance had the least recession in lowest live limb and base of the balanced live crown, while the Idaho and Washington provenances had the most. Utah and British Columbia trees were intermediate in crown recession. The height of the lowest live limb and the general recession of crowns in sapling stands of lodgepole pine are of more than passing interest to field foresters. Early thinnings for stocking control are sometimes ineffective, due to branch turnups, when lower live limbs or viable branch buds exist below the stump height that can be practically attained in thinning. In most areas, foresters have determined by experience the minimum stand age and practical stump height for avoiding the branch-turnup problem; however, if the persistence of the lowest live limb is under genetic influence as suggested by these results, it should be considered in tree improvement and planting programs. Likewise, crown recession has become increasingly important in relation to hiding and thermal cover for wildlife, and should be considered in seed transfer decisions.

Stem diameters were measured at breast height (4.5 ft [1.37 m]) for the first time at year 12 and, when adjusted for seedling height when planted, were found to vary significantly among the provenances. Diameters of Idaho trees were significantly greater than those of British Columbia and Utah, while Montana trees were significantly larger than those of Utah (p values < 0.10). Washington trees were intermediate in breast height diameter, but were not significantly different than the other provenances.

Because the provenances studied here represent widely separated geographic locations and a considerable range of elevations, we expected appreciable differences (as were noted) in the means of most traits measured in this study. Rehfeldt and Wykoff (1981) found that growth differences among Montana and Idaho lodgepole pine populations

were more a result of adaptation to length of growing season than to growing season temperature alone. Further, Rehfeldt (1986) developed methods for separating the relative influences of elevation and geography on various heritable traits of lodgepole pine in eastern Idaho and western Wyoming. From these he estimated that elevation accounted for over 70 percent of the variance in five shoot-elongation variables, while geography accounted for less than one-third of the variance. A conclusion drawn in both of these studies (Rehfeldt 1986; Rehfeldt and Wykoff 1981) is that successful transfer of lodgepole pine populations from their origins is largely a matter of balancing the traits of nondormant cold hardiness and capacity for late growth (shoot elongation after the fourth week); and that these traits are considerably more influenced by elevation than by geography. In this vein, populations from lower elevations were found to have considerably greater capacity for late growth than high elevation populations, but this made their seasonal growth more vulnerable to late-growing-season frosts.

Referencing the elevation and geographical location of the study plantation to elevational and geographical differences of the five provenances reported in this study (table 1), we would expect that the low-elevation (2,300-ft [700-m]) British Columbia seed source would have the greatest growth capacity, but be more vulnerable to growth attrition due to cold damage. Observance of some decline in performance of the British Columbia provenance from age 7 to age 12, relative to other provenances, suggests that this is the case, and as the trees have now grown beyond the snow level, maladaptation to this cold site is offsetting the earlier growth advantage of the British Columbia provenance. At the other elevation extreme, the Utah provenance would be expected to be relatively limited in its growth capacity on the lower elevation Montana test site, as was observed. The elevationally intermediate Idaho and Washington provenances, although of essentially the same elevation, have developed somewhat differently in this study. Generally, the Idaho trees have become as large, or larger, than all other provenances in height, diameter, and crown width—and show the greatest degree of crown recession. The Washington trees have developed less than the Idaho trees in all traits measured, but with the exception of crown width, the differences are not statistically significant. Trees from the local Montana seed source exhibited intermediate development in relation to the other provenances, except for crown recession in which Montana trees exhibited the least change.

The provenances tested here differed in among- and within-family variation. The Montana families showed the least and Washington the most among-family variation, of the four provenances where seed was collected from a restricted area and elevation. The Utah provenance could not be compared in this regard because families were collected from an elevational range of nearly 1,000 ft (290 m); thus, a large amount of the among-family variation was attributed to elevational differences. The pattern of within-family variation among provenances differed from trait to trait in this study, with the exception of the Utah trees which exhibited consistently the highest within-family variation. Because variation within family is not as likely as among-family variation to be influenced by elevation, this suggests that lower latitude-higher elevation lodgepole pine populations, such as in Utah, might possess greater within-family variation than more-northerly populations. This, as well as some of the other questions raised by this study, will perhaps be answered by long-term lodgepole pine provenance trials (involving more populations from each provenance than this study) that are now established throughout the Northern Rockies.

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Survival and development of progeny from lodgepole pine seed from British Columbia, Washington, Idaho, Utah, and a local population were observed after 12 years in a provenance trial conducted on a high-elevation site in southwestern Montana. Differences among provenances were not significant for survival, but were significant for developmental traits. The Idaho provenance showed the greatest growth, the Utah provenance the least. Among-family variation was greatest in the Washington provenance; within-family variation was greatest in the Utah provenance.

KEYWORDS: progeny testing, seed transfer, *Pinus contorta*

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